

BIOLOGY OF *POLISTES ANNULARIS*  
(HYMENOPTERA: VESPIDAE)  
I. SPRING BEHAVIOR

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Although the social biology of several polistine wasps has been discussed in considerable detail by Bequaert (1923), Eberhard (1969), Evans and Eberhard (1970), Isely (1922), Pardi (1948), Rabb (1960), Rau (1931, 1933, 1939) and Spieth (1947), relatively little has been reported on *Polistes annularis* L. (Rau, 1940). *P. annularis* is the most common paper wasp around the Athens area. It is pleometrotic (=polygynic=cooperative cofounding) (Bequaert, 1923; Rau, 1940; Reuter, 1913; Wasmann, 1910) in its behavior and in being such is an excellent subject for the study of dominance reactions in social insects.

We began our studies on this species in the spring of 1970, and we collected detailed information on all of the life stages and seasonal activity through June of 1971. Additional data was collected on occasion through the active season of 1974. Our findings differ in some respects from those of Rau (1940), who studied *P. annularis* in the midwest, and Rabb (1970), who investigated polistine species in the Raleigh, N. C., area. The predominant polistine species in Rabb's area were *P. exclamans* and *P. fuscatus*.

Because we have collected a considerable amount of information, we have decided to consider each phase of the seasonal history of *P. annularis* separately and publish this information in series form. The serial reports will be three in number, dealing with behavioral periods of the 1) Spring, 2) Summer and 3) Fall-Winter-Spring. The present report, the first of the series, deals with Spring behavior. We previously reported on the anatomy and function of the venom apparatus and sternal glands in this and other vespid species (Hermann and Dirks, 1974; Hermann and Krispyn, 1975; Hunt and Hermann, 1970) and on the cohibernation of five polistine species (Hermann, Gerling and Dirks, 1974).

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## MATERIALS AND METHODS

A large barn on the edge of Athens, Ga., was selected as the main site for investigation because it harbored one of the best populations of *P. annularis* in the area (Fig. 1). Although several polistine species nested there, *P. annularis* was the predominant species with *P. hunteri* and *P. exclamans* next in abundance. Abandoned houses and other barns also were investigated, as well as nests in shrubs and bushes.

Cofounding females were marked on the thoracic dorsum with rapid drying model paints of various colors and combinations of colors. Marking was most often done at night with no aggressive occurrences. Similar marking of workers was more difficult.

Cofounding females were watched daily, their presence and absence from the nest being recorded. Any new arrivals from one nest to another could be spotted immediately due to the different colors used in marking. All of the behavioral characteristics were observed repeatedly on numerous nests to assure that they were routine in the life of *P. annularis*.

Dominance reactions were carefully investigated on separate nests where each cofoundress could be marked differently. Upon behaviorally determining the dominant cofoundress (queen) the wasps of a number of nests were taken and dissected for an investigation of their reproductive systems (Dirks and Hermann, 1975a).

Observations on nest size increase and immature stages were made at night since the nest could be approached with ease during early colony development, prior to the emergence of workers. Also, much of the information on the number of adults on a nest and the identity of females on a nest was obtained at night.

## RESULTS AND DISCUSSION

*P. annularis* clearly demonstrates seasonal colonial changes while its relative, *P. canadensis*, apparently shows no seasonal synchrony in the foundation and termination of colonies in tropical areas where no temporal changes occur (Eberhard, 1969).

## PRE-NESTING AGGREGATIONS

In the beginnings of nest establishment by *P. annularis*, certain behavioral characteristics are carried over from a pre-nesting or post-hibernation period (Hermann and Dirks, 1975). The fertilized females from the previous year show strong tendencies to aggregate into groups of individuals having similar origins (sibling relationship).

Although they form aggregations, each adult wasp is an individual which functions almost independently from other wasps in the aggregation (i.e., no individual forms a "nucleus" as with the queen honey bee). This independence remains to some extent throughout colony life, although each wasp on a nest influences and is influenced by the other co-foundresses of the colony.

In addition, the establishment of dominance hierarchies begins during the pre-hibernation period in late fall (at the end of the nesting period) and continues through the post-hibernation period of early spring (Hermann and Dirks, 1975). These hierarchies later are instrumental in determining nest duties (division of labor among colony cofoundresses). Dominant females remain at the "parent site" and because of this struggle for dominance some of the cofoundresses are forced to disseminate. Each dominance hierarchy has, within its own structure, characteristic behavioral patterns that are present regardless of colony size.

#### DOMINANCE HIERARCHIES

Each colony of these pleometrotic females commences under the pressure of dominance establishment. Such establishment often involves up to eight or ten females (cofoundresses) which are all making an attempt to become the dominant queen of the colony (alpha individual of Pardi, 1948). Although single *Polistes canadensis* females have been reported by Eberhard (1969) to most often initiate a nest alone, similar to the fashion demonstrated by *P. fuscatus*, Rau (1933) has described colony founding by several *P. canadensis* nestmates (siblings) that were chased from their original nest. The females of *P. annularis*, a close relative of *P. canadensis*, readily initiate their nests with a number of females. However, like with *P. canadensis*, additional females often join the *P. annularis* nest after initiation (Rau, 1940).

A colony usually benefits by having a number of cofoundresses rather than a single queen, but maximum efficiency is not achieved because of dominance struggles. As an example, by April 15, 1971, nest #18 occupied by a single queen had 6 cells. On the same date nests #16 and #17 with multiple queens (2 and 5 respectively) had 11 and 13 cells respectively; the number of cells, however, is not in proportion to the number of cofoundresses present. If the number of cofoundresses could be directly correlated with the cells present in a nest, we would expect nest #16 to have 12 cells on April 15 and nest #17 should have 18 on the same date. In addition,

with proper division of labor among cofoundresses we would expect an even higher number of cells. This is not the case; there is a loss in efficiency due directly to dominance reactions on the nest, which we will discuss later. Larger nests also are produced in colonies by both *P. fuscatus* and *P. canadensis* when foundress associations are large.

Bequaert (1923) and Isely (1922) reported similar findings in their investigations of *P. pallipes* and *P. metricus* respectively, although an efficiency loss was not as apparent in colony founding by either of these species. Rau (1940) found highly significant differences in cell numbers of single versus multiple cofoundresses in his studies of *P. annularis*.

### COFOUNDRESS CHARACTERISTICS

Several anatomical and behavioral characteristics are demonstrated by each cofoundress. Each such female 1) is a fertile producer of diploid eggs (Dirks and Hermann, 1975a); she attempts to establish her dominance by 2) demonstrating unilateral aggressiveness toward other cofoundresses (i.e., biting, over-under posture, stinging); and 3) she is capable of rigid gastral movements, known as abdomen (tail) wagging (Eberhard, 1969).

Insemination the previous fall or in the following spring (Hermann, Gerling and Dirks, 1974) appears to be quite successful in this species. All of the females examined on nests in the early days of colony establishment were found to be fertile and all were found to be depositing eggs (Dirks and Hermann, 1975a). However, in the struggle for dominance, a significant amount of oophagy persists until a more stable nest is established.

### OOPHAGY AND COOPERATIVE EGG DEPOSITION

Recognition of oophagy is facilitated by the deposition of eggs near the cell surface after the wasp has ingested an egg. As the cells of a nest are elongated the eggs are deposited further and further from the cell base. The finding of eggs deposited a considerable distance from the cell base during the period of early nest building is a definite sign of oophagy. Oophagy will continue in an early colony until about the time that larvae appear.

Each cofoundress seems to demonstrate oophagy. Likewise, in an early examination of reproductive systems, it was found that every female on a nest in the beginning stages of colony founding was depositing eggs (Dirks and Hermann, 1975). Hence, after oophagy

Table 1. Average data from *P. annularis* nests with multiple cofoundresses, 1970.\*

Date	# of Cofoundresses	# of cells present	# of capped cells	# of workers
April 16	3	13.33	0	0
17	2.33	14	0	0
18	2.33	16	0	0
22	2.33	21	0	0
23	2.33	24	0	0
26	2.0	24	0	0
May 1	2.0	32.33	0	0
13	2.33	41.5	0.33	0
20	2.33	44.33	8	0
22	2.33	46	11.33	0
27	2	50.67	16	0
June 16	2	80	14	16***
17	1**	—	13.5	13.5

\*Nests #17, 19 and 20.

\*\*Initial loss of first cofoundresses and emergence of workers.

\*\*\*First emergence of workers, leading to interactions between new workers and colony cofoundresses.

by a female she immediately deposits her own egg, thus resulting in a very inefficient waste of time and energy on the part of colony building. According to Eberhard (1969) only one egg-laying female of *P. canadensis* was ever present on a nest at any one time. Consequently, differential oophagy was not observed in this species.

Such an efficiency loss in the early colonies of *P. annularis* is recognized by the slow process of cell building in the early stages of nest construction in which several cofoundresses are involved. As dominance is established by the dominant queen, subordinate cofoundresses put more time into colony duties (become workers or beta individuals) and the building of cells increases.

Table 1 illustrates an average of 3 *P. annularis* nests in which there are only about 2 cofoundresses per nest. Whenever there are only 2 or 3 cofoundresses present dominance is established at an early stage of nest development and there is not as evident an efficiency loss as we find on larger nests.

A decrease in colony activity was reported for *P. canadensis* by Eberhard (1969) although it apparently did not represent a loss in efficiency. During a five-week period of early nest founding there were no new cell building and no observed oviposition. Eggs and larvae also developed at a reduced rate.



## AGGRESSIVENESS TOWARD COFOUNDRESSES

Unilateral aggressiveness is evident even before colony initiation. Much like the behavior of *P. gallicus* (L.) (Pardi, 1948), there is a lack of equivalence between females, certain females apparently showing dominant characteristics from the start. Likewise, a female that appears dominant never loses her dominant position on the nest. Females attack each other in the pre-hibernation and early post-hibernation clusters (Hermann and Dirks, 1975). Such aggressiveness may involve a rapid darting of one female toward another. In many cases, aggressive attacks result in the entanglement of a wasp's legs with those of the other wasp and the subsequent falling to the ground by these individuals while attempting to bite and sting.

On occasion, we have found individuals that were stung, although most encounters merely result in some establishment of dominance by one of the fighting pair without bodily harm. Both wasps most often take flight after such an encounter and either return to the cluster (in the case with the dominant wasp and often the subordinate one also), or retreat to a new location. As with *P. canadensis* (Eberhard, 1969), subordinate cofoundresses that actually were attacked by the dominant female often left the colony. Subordinate *P. canadensis* females that remained on the nest became idle residents; however, subordinate *P. annularis* females became workers (beta individuals of Pardi, 1948).

We believe that the females remaining in these clusters are the ones that commence a pleometrotic colony while the most subordinate females (the ones that fly away from the clusters) often establish small colonies as single queens, sometimes later to be joined by other cofoundresses. In most cases, females that initiated their nest building alone never completed their nest; the nests never got to be larger than a few cells and the nests eventually were abandoned.

During colony initiation, subordinate females that initiate their own colonies singly are occasionally replaced by new dominant females that arrive after a small nest with several cells has been constructed. On occasion, we have even seen *P. annularis* queens replaced by a *P. exclamans* queen (possible beginning of an allometrotic association), although colony life ceases to function when there is such an aggregation of two species.

In other cases, nests with single or multiple foundresses may pick up additional females that come from other nests. In the latter case, these females either come from nests that they were chased from or from a nest of sibling females (females that originated from the same

nest the year before). Several nests in our study area had sibling wasps that originated from the same nest the year before.

There was an extensive exchange of wasps between some of the nests that were established by sibling females. Wasps occasionally were also found to join females on unrelated nests. During the exchange of wasps on nests, acceptance of these females by the original females usually was the case, although there is more exchange among sibling than unrelated wasps. Apparently, there is not much exchange of wasps between the nests of *P. canadensis* (Eberhard, 1969).

Unilateral aggressiveness continues to a lesser degree in later stages of colony building. Usually, the dominant queen demonstrates a dominant posture over her peers and upon approaching these peers she often moves rapidly toward them in a jerky aggressive manner.

#### CHARACTERISTICS OF A DOMINANT FEMALE

Once dominance is established by a single female, certain behavioral and anatomical changes occur in her and in the subordinate females. Anatomically, the reproductive system of the dominant female increases in size and she is able to increase her egg production. Simultaneously, the reproductive system of the subordinate females atrophies and they commence functioning as workers (Dirks and Hermann, 1975a; Pardi, 1948).

Behaviorally, the dominant female begins to "tail wag," a phenomenon not well understood at this time. Tail wagging may be demonstrated by a number of individuals on a nest or just by the dominant female. Workers also have been seen tail wagging on numerous occasions. When several cofoundresses all tail wag it always is the dominant female that is outstanding in her demonstration of it.

Tail wagging produces several results: 1) it points out the dominant female and the subsequent subordinates; 2) it helps maintain a position for the tail wagging female in the dominance hierarchy; 3) it appears to increase nest activity either audibly or visually; 4) it indicates that workers really do enter into dominance reactions with fertile cofoundresses and other workers.

The dominant female checks the cells periodically, and thus she investigates the larvae and deposits eggs in the new cells. This female also is responsible for most of the "smearing" (Hermann and Dirks, 1974). She spends much of her time on the face of the nest during the day but at night she may either be on the face or on the nest pedicel.

Subordinate females check the cells periodically but do not deposit eggs in them. They feed the larvae material brought in by them or by other cofoundresses. They also "smear" to some degree, although most of this is done by the queen (Hermann and Dirks, 1974).

It is obvious at this stage that the subordinate cofoundresses become workers (beta individuals, Pardi, 1948), in spite of the fertile condition of their spermatheca. They are subordinate to a single dominant queen (alpha individual). The establishment and maintenance of a well defined dominance hierarchy takes as long as two and a half months, until the first emerging workers arrive.

The emergence of workers further complicates the dominance hierarchy since workers begin competing with the subordinate cofoundresses for dominance and the workers evidently put the cofoundresses under extensive pressure at this time (about June 16, Table 1); with the appearance of the first workers, the subordinate cofoundresses leave the nest, never to return, leaving only the dominant queen and workers (new beta individuals) on the nest. Workers begin to "tail wag" to some degree and "smear," behavior normally demonstrated by the queen or cofoundresses. The leaving of the subordinate cofoundresses is a strong indication of their extremely subordinate position in the colony. It appears that once a cofoundress becomes subordinate it will be dominant to no wasp, except those already subordinate to her, including a worker. The queen (dominant cofoundress) usually remains on the nest through August but leaves the nest permanently long before cold weather. According to Pardi (1948), the queen (representing the alpha individual on the nest during most of the nest life) shows a lower dominance frequency upon growing old but maintains supremacy on the nest until later in the season. Rau (1939) indicated that his observations of *P. annularis* colonies likewise revealed first the arrival of workers and a subsequent departure of subordinate cofoundresses.

Pardi (1948) reported that after the eclosion of *P. gallicus* workers and the elimination of auxiliary females (if the queen dies), a worker that is in the beta position on the nest begins to dominate its siblings and soon begins to deposit eggs. Rau (1931) also mentions egg deposition by workers when the queen is lost. Pardi does not mention the pressures of the dominance hierarchy as being put on colony cofoundresses, thus resulting in their permanent departure from the nest.

The build up and atrophy of colony life encompasses approximately five months. This is much the same as the cycle found in colonies of *P. canadensis* (Eberhard, 1969). Colony enlargement ceases when



the queen leaves the nest. Loss of the queen occurs in April for *P. canadensis* and in late August for *P. annularis*.

#### SELECTION OF A NEST SITE

*P. annularis* females most often select a nest site near or on the nest site from the previous year. In the Athens area this is on and in buildings. Very little nesting occurs in trees, shrubs or bushes. Of the nests found in shrubs and bushes, none appeared to last through a complete season. After their posthibernation aggregating and mating they go to or near the nest site occupied by the nest from which they emerged. If the old nest still remains, they may begin construction of a new nest near the old nest or on rare occasions even on the face of the old nest. If the old nest has been removed, the new nest most often is started directly on the old pedicel or on the exact spot that the old nest occupied. Never is the old nest used again.

The reasons for not using the old nest are several. The old nest is often torn and dirty. These problems, however, could be handled by repair and cleaning. Probably the most important consideration is that many of the nests are parasitized by late summer and the parasites sometimes overwinter in the nest. The old nests, thus, would have built-in parasites which would be highly detrimental to a colony. Also many nests have overwintering moths that prey on the immature stages of polistine wasps.

#### COLLECTION OF WOOD FIBER

From the beginning of nest establishment, the dominant queen remains on the nest most of the time while her cofoundresses collect wood and build the nest. Wood is collected most often from old buildings by scraping surface wood off with the mandibles. This wood pulp is mixed with saliva and added to the nest in a characteristic way (Eberhard, 1969). As dominance is established and workers emerge, the functions of wood gathering and nest building are assumed by them.

#### COLLECTION OF FOOD

As in wood gathering and nest building, the dominant queen devotes very little time to the collection of food. On nests with only 2 or 3 cofoundresses, the dominant female may leave on occasion but as dominance is better established she ceases functioning away from

the nest. Food supplied to an early nest usually is the function of the subordinate cofoundresses. When workers emerge they assume this duty.

Rabb (1960) put together an extensive list of prey collected by workers of *P. annularis*. It included 16 families of Lepidoptera and a few records of prey from the orders Diptera, Hemiptera, Homoptera, Hymenoptera and Orthoptera, as well as a few spiders. About 20% of the wasps, returning to the nest had some type of prey while most returned with liquid.

Rabb also reported that 85% of the prey collected was gotten from wooded areas while the remaining prey was taken in fields. This is in contrast to the collecting of some other polistine species (e.g., *P. fuscatus* and *P. exclamans*) that collect most of their prey in fields.

### COLONY PROTECTION

Nests and the inclusive immature stages are protected in a number of ways: 1) repellent compounds are routinely smeared on the nest pedicel (Hermann and Dirks, 1974); 2) adult wasps rest in a characteristic defensive fashion at night; 3) a defensive posture is readily assumed by females when a nest is approached; 4) along with a defensive posture the prothoracic legs and possibly the antennae and wings are moved in such a way as to represent a warning mechanism; 5) darting at small intruders is occasionally seen; 6) adult wasps, especially workers, will aggressively attack an intruder.

*Defensive Smearing* — Hermann and Dirks (1974) have reported smearing by a number of polistine wasps and the possibility of smearing by all vespids. Smearing is accomplished by the rubbing of the gastral sternites on the structure to be smeared (usually the nest pedicel). The glands that produce the repellent compounds are found inside the hemocoel immediately above gastral sternites 6 and 7. The glands consist of numerous unicellular structures, each joined to the sternite base by a single filamentous duct. The sternite has a dispenser brush to facilitate the smearing process.

The smearing compounds evidently are volatile since smearing takes place periodically throughout the day. Detection of the compounds or lack of them appears to be accomplished with the antennae. Double smearing appears to occur often and may be the result of detecting more of the smearing compound on one side of the pedicel than the other. Occasionally, the pedicel is worked with new wood fiber. The mandibular gland may play a role here in adding a different and possibly a synergistic repellent compound to the nest base.

Although smearing has been seen in only a few species of the Polistinae, sternal glands and sternal brushes have been found in many vespids. It is possible that *Vespula* species smear on the structures to which their nest adheres.

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